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Optimal visuo-tactile integration for velocity discrimination of self-hand movements

M. Chancel [1, 2], C. Blanchard [3], M. Guerraz [2], A. Montagnini [4*], A. Kavounoudias [1*]

[1] Aix Marseille Université, CNRS, LNIA UMR 7260, FR3C,13331 Marseille, France

[2] Université Savoie Mont Blanc, CNRS, LPNC UMR 5105, F-73000 Chambéry, France

[3] University of Nottingham, School of Psychology, NG7 2RD Nottingham, UK

[4] Aix Marseille Université, CNRS, INT UMR 7289, 13385 Marseille, France

* A.M. and A.K. contributed equally to this work.

Corresponding author

Dr. Anne Kavounoudias

Aix-Marseille Université - CNRS

Laboratoire de Neuroscience Intégrative & Adaptative (UMR7260)

3 Place Victor Hugo - 13003 Marseille – France

Phone : +33 413 550 836

Fax : +33 413 550 844

e-mail : Anne.Kavounoudias@univ-amu.fr

Running Head: Optimal visuo-tactile integration in kinesthesia

Author contributions

All the authors conceived and designed the experiment; MC & CB performed the experiments, MC analysed data; MC, CB, AM & AK interpreted results of experiments; AM conceived the model; MC & AK drafted the manuscript; All the authors revised the manuscript.

Abstract

Illusory hand movements can be elicited by a textured disk or a visual pattern rotating under one's hand, while proprioceptive inputs convey immobility information (Blanchard et al., 2013). Here we investigated whether visuo-tactile integration can optimize velocity discrimination of illusory hand movements in line with Bayesian predictions. We induced illusory movements in fifteen volunteers by visual and/or tactile stimulation, delivered at six angular velocities. The participants had to compare hand illusion velocities with a 5°/s hand reference movement in an alternative forced choice paradigm. Results showed that the discrimination threshold decreased in visuo-tactile condition compared to unimodal (visual or tactile) conditions, reflecting better bimodal discrimination. The perceptual strength (gain) of the illusions also increased: the stimulation required to give rise to a 5°/s illusory movement was slower in the visuo-tactile condition compared to each of the two unimodal conditions. The Maximum Likelihood Estimation model satisfactorily predicted the improved discrimination threshold, but not the increase in gain. When we added a zero-centered Prior, reflecting immobility information, the Bayesian model did actually predict the gain increase, but systematically overestimated it. Interestingly, the predicted gains better fit the visuo-tactile performances when a proprioceptive *noise* was generated by co-vibrating antagonist wrist muscles. These findings show that kinesthetic information of visual and tactile origins is optimally integrated to improve velocity discrimination of self-hand movements. However, a Bayesian model alone could not fully describe the illusory phenomenon pointing to the crucial importance of the omnipresent muscle proprioceptive cues with respect to other sensory cues for kinesthesia.

Key-words: Illusions, Bayesian modeling, Kinesthesia, Multisensory integration, Muscle proprioception

New & Noteworthy

The present study demonstrates for the first time that kinesthetic information of visual and tactile origins are optimally integrated (Bayesian modeling) to improve velocity discrimination for self-hand movement. We used an original paradigm consisting in similar illusory hand movements induced through visual and tactile stimulation. By testing the role of other sources of information favoring non-moving hand perception we also highlight the key contribution of the omnipresent muscle proprioceptive information and its over-weighting for kinesthesia.

Introduction

To perceive our body movement in space, we can rely on several sensory inputs. Among them, the involvement of muscle proprioception in kinesthesia has been widely investigated (for reviews see McClosckey, 1978; Roll et al., 1990; Proske and Gandevia, 2012). The visual system also contributes to the sense of movement, as evidenced by vection phenomenon, i.e. a kinesthetic percept elicited by a visual moving scene scrolling in front of a participant (Brandt and Dichgans, 1972; Guerraz and Bronstein, 2008) or under one's limb (Blanchard et al., 2013). Touch, like vision, also conveys kinesthetic information with cutaneous receptors sensitive to the velocity of superficial brushing applied to their receptive fields (Breugnot et al., 2006). Illusions of self-body movements can thus be induced using a tactile stimulus rotating under the palm of the hand (Blanchard et al., 2011, 2013).

However, less is known about how these two sensory modalities interact to estimate self-body motion. Many studies highlighted a perceptual benefit when two or more sensory signals are combined, provided they are temporally and spatially congruent. Based on a probabilistic representation of information and on the assumption that minimizing the variance of the combined perceptual estimate is a primary goal of multisensory integration, the Optimal Cue Combination framework has provided an efficient approach to predict the perceptual enhancement due to

multisensory integration (Landy et al., 2011). In particular, the Maximum Likelihood Estimation (MLE) principle postulates that the multisensory estimate of an event is given by the reliability-weighted average of each single-cue estimates (where reliability is defined as the inverse of variance). MLE predictions have been successfully reported for several multisensory tasks, but mainly when the object of perception is external to the body (Ernst and Banks, 2002; Alais and Burr, 2004; Wozny et al., 2008; Gingras et al., 2009; Gori et al., 2011). Whether Bayesian rules can account for multisensory integration subserving self-body perception has been less investigated, especially with regard to the integration of visuo-tactile kinesthetic cues. Visual and vestibular information were found to be close-to-optimally integrated in the perception of whole-body displacements (Fetsch et al., 2009; Vidal and Bülthoff, 2009; Prsa et al., 2012); as vision and proprioception when evaluating arm movements (Reuschel et al., 2009), positions in space (VanBeers et al., 2002; Tagliabue and McIntyre, 2013), as well as when performing pointing motor tasks (Sober and Sabes, 2003, 2005).

The present study aimed at further investigating whether visual and tactile signals are optimally integrated when estimating self-hand movements. During natural movements, muscle proprioceptive afferents are continuously activated and they cannot be selectively removed without impairing concomitant cutaneous afferents (for instance, an ischemic block affects all large somatosensory fibers, including both cutaneous and proprioceptive fibers (Diener et al., 1984). Therefore, it is usually impossible to estimate the kinesthetic contribution of visuo-tactile modalities independently from muscle proprioception. For this reason, we induced illusory movements rather than actual movements using a visual and/or tactile moving background rotating under the hand, i.e. the participants felt that their hand was passively rotated though it remained perfectly still. We estimated the perceptual benefit of visuo-tactile stimulation compared to each unimodal stimulation in a discriminative test of self-hand movement velocity, and then compared it to the MLE predictions.

However, in our experiment, participants were aware that their hand was not actually moving, and this cognitive component was further strengthened by a proprioceptive feedback from the wrist muscles conveying static information. This Prior knowledge combined with static muscle

proprioceptive cues might explain why the perceived velocity of the illusory movements was about six times less than the actual velocity of the stimulation (Blanchard et al. 2013). In the Bayesian framework, sensory illusions have been successfully explained as the result of an optimal combination between noisy sensory information and stimulus-independent Prior knowledge. For example, a Prior favoring low-speed motion can account for several visual illusory phenomena observed in motion vision (Weiss et al., 2002; Montagnini et al., 2007). Studies about self-body perception used a Gaussian low-speed Prior distribution to account for top-down expectations that influence perceptual performance (Jürgens and Becker, 2006; Laurens and Droulez, 2006; Dokka et al., 2010; Clemens et al., 2011).

Therefore we tested a Bayesian model including a Gaussian Prior distribution, as well as a proprioceptive Likelihood, both centered on zero, in order to account for the strong belief in favor of immobility and for the omnipresent static information from muscle spindle endings. The combination of these two Gaussian distributions centered on zero should provide a theoretical ground for the very low gain of the illusory hand-motion perception. For the sake of simplicity, we will refer to this combined information as zero-centered Prior. We also manipulated this Prior static information by disturbing proprioceptive feedback. To this end, we equally applied a co-vibration onto the participants' antagonist wrist muscles (*Noisy* condition). We expected to make the muscle proprioceptive inputs less reliable, and consequently to lower the weight of the static information taken into account in the Prior distribution and to increase the gain of illusory perception.

Method

Participants

Twenty right-handed volunteers (14 women) with no history of neurological disease agreed to participate to this study. They all gave their informed consent, conforming to the Helsinki declaration,

and the experiment was approved by the local Ethics Committee (CCP Marseille Sud 1 #RCB 2010-A00359-30). Five of them did not experience any illusory perception during the tactile stimulation and were therefore not included in the complete series of experiments and analysis.

Stimuli (Fig. 1)

Tactile stimulation was delivered by a motorized disk (40 cm in diameter) covered with cotton twill (8.5 ribs/cm), which is a material known to efficiently activate cutaneous receptors (Breugnot et al., 2006). The disk rotated under the participant's right hand in a counterclockwise direction with a constant angular velocity ranging from 10 to 45 °/s (Fig. 1B).

Visual stimulation consisted of a projection of a black and white pattern on the disk. To give the participant the feeling that the pattern was moving in the background, i.e. under his/her hand, a black mask adjusted to the size of each participant's hand was included in the video and prevented the pattern from being projected onto his/her hand. The pattern was rotating around the participant's right hand with a constant counterclockwise angular velocity ranging from 10 to 45 °/s (Fig. 1C).

These two types of stimulation were delivered for six seconds either separately (unimodal conditions) or simultaneously (bimodal condition) at six different velocities (10, 20, 25, 30, 35, and 45 °/s). These stimulation velocities were chosen based on a previous study (Blanchard et al., 2013) to induce efficient illusory movements with a perceived velocity well distributed around 5 °/s (reference velocity).

In the *Noisy* conditions, muscle proprioception was disturbed using low amplitude mechanical vibration (0.5 mm peak-to-peak) set at a constant low frequency (20 Hz). We used two vibrators each made of a biaxial DC motor with eccentric masses forming a 5-cm long and 2-cm in diameter cylinder. As shown on Figure 1D, they were fixed on both sides of the participant's right wrist to stimulate equally and simultaneously two antagonist muscle groups: the *longus pollicis* and the *extensor carpi ulnaris* muscles. Indeed, microneurographic studies showed that such low amplitude vibration preferentially activates muscle spindle primary endings. Roll et al (1989) have shown that in 10 to 100

Hz vibration range, primary muscle spindle endings respond with a frequency of discharge equal to the vibration frequency (with a 1 : 1 mode of response), resulting in a masking effect of spontaneous natural discharges, usually ranged between 3 to 15 Hz in the absence of vibratory stimulation (Roll et al., 1989). When applied onto a single muscle group, vibration stimulation can elicit an illusory sensation of limb movement but any illusion is cancelled when a concomitant vibration is equally applied onto antagonist muscles (Calvin-Figuière et al., 1999). Therefore, by equally co-stimulating wrist antagonist muscles, we expected to disturb proprioceptive afferents without inducing any illusory sensation of movement. The stimuli were delivered using a National Instruments card (NI PCI-6229) and a specifically designed software implemented in LabView (V.2010).

Insert Figure 1 around here

Procedure

Participants sat on an adjustable chair in front of a fixed table with arm-rests immobilizing their forearms, their left hand resting on the table and their right hand on the motorized disk. A small abutment in the disk center placed between their index and middle finger kept their hand from moving with the disk when it rotated. Head movements were limited thanks to a chin- and chest-rest allowing participants to relax and sit comfortably. The experiment took place in the dark and participants wore headphones to block external noise, as well as shutter glasses partially occluding their visual field and reducing it to the disk surface only.

Training phase

Before the experimental session, each participant underwent two training sessions. First, a 15 minute session consisted of 150 trials of separate tactile and visual stimulation applied at medium velocity (25 °/s). To be included in the experiment, the participants had to feel illusory hand rotations in at least 80 % of the trials.

178 Then, the participants were trained to perform a reproducible 5 °/s clockwise hand rotation. During this
179 second 15 minute session, with their middle fingers they had to follow a red line moving at 5 °/s that
180 was repeatedly projected onto the disk every 7.5 seconds. Participants were asked to memorize the
181 movement using all the available information (tactile, visual and proprioceptive feedback, plus efferent
182 motor command). This 5 °/s movement was chosen as the reference to which participants would have
183 to compare their perception during the discrimination test phase.
184
185
186 *Discrimination test phase*
187 The experimental test consisted of a 2-AFC (alternative forced choice) discrimination
188 task with constant stimuli. A stimulation condition (visual, tactile or combined) and the
189 reference movement were presented by pairs in random order. The participants were instructed
190 to say out loud whether the illusory movement they perceived was faster or slower than the
191 reference movement.
192 The reference movement executed during the experimental test was similar to that performed
193 during the training phase except that the red line appeared only during the first and the last of the 6
194 seconds of the movement duration to prevent the participants from using only visual feedback.
195 Three stimulation conditions were randomly intermixed within the experimental sessions: two
196 unimodal conditions (tactile T, visual V) and one bimodal condition (visuo-tactile VT). For each
197 stimulation condition, 6 intensities were tested and presented immediately before or after the reference
198 movement. All stimuli lasted 6 seconds (as the reference movement) and the inter-stimulus intervals
199 ranged between 1.7 and 2.3 seconds. Before each reference/stimulation pair, a white line was projected
200 to make sure that participants always positioned their hand in the same orientation. Participants were
201 instructed to focus on their hand to estimate as accurately as possible whether the illusory movement
202 they perceived was faster or slower than the reference movement they executed just before or just after
203 each stimulus. They had to keep their eyes open, except if a green screen appeared signaling them to

close their eyes before a tactile-only stimulus. At the end of each pair (reference/stimulation) presentation, participants had 2 seconds to answer ("*faster"* or "*slower"*) and 3 seconds (± 300 ms) before a new pair was presented. The presentation order of the 18 stimulation conditions was counterbalanced for each subject.

During the *Standard* condition test, participants were asked to compare 270 reference/stimulation pairs (3 conditions * 6 intensities * 15 trials) divided into four sessions of 10 minutes each performed on two different days (at the same time during the day). Thirteen of the fifteen participants were tested in four additional *Noisy* condition sessions of 10 minutes during which the same block of 270 pairs of reference/stimulation was presented while participants underwent co-vibrations of their antagonist wrist muscles.

Movement acquisition and kinematic analysis

Participants were asked to compare the velocity of each illusory movement they experienced during the unimodal and bimodal stimulation conditions with the velocity of the same reference movement, consisting of a clockwise rotation of the right hand at 5 °/s that they actively performed just before or just after every stimulus. All reference movements were recorded using an optical motion capture system (CODAmotion, Charnwood Dynamics, Rothley, UK) composed of 3 infrared 'active' markers and one camera to track the 3D marker positions (sampling frequency: 10 Hz). Markers were attached to the participants' middle finger, on the top of their hand back, and on the last third of their forearm to capture the angular rotation of their wrist during the reference movement execution.

For each participant, the mean angular velocity of hand movements was extracted with the Codamotion Analysis software (V6.78.2). Reproducibility of the reference movement across the 270 trials during the *Standard* experiment was further tested by a one-way ANOVA for each participant with the session (4 sessions) as experimental factor for the *Standard* condition (without vibration) and the *Noisy* condition (with co-vibration stimulation). As expected, no significant difference in the mean velocity of the reference movement was found between sessions whatever the participant neither in the

Standard nor the *Noisy* condition. Note that individual variability estimated from the four sessions ranged between 0.22 and 0.37 °/s. We further verified the precision of estimation of the reference movement in a complementary experiment performed on ten naïve participants consisting in a discrimination task between several self-hand rotations actively executed. Participants were asked to compare the velocity of the fixed reference movement set at 5°/s (like in the main experiments) with 8 other hand movement velocities (3.5°/s, 4 °/s, 4.5 °/s, 4.75 °/s, 5.25 °/s, 5.5 °/s, 6 °/s, or 6.5 °/s). Again, the estimated variability was found to be small (ranging from 0.33 to 0.79 °/s).

A one-way ANOVA was also performed to ensure that reference movement was not significantly different between participants (*Standard* condition: $F(3, 42) = 1.05$, $P = .38$; Noisy condition: $F(3, 36) = 0.21$, $P = .89$). Finally, a Student's paired *t* test was used to ensure the reproducibility of the reference movement between the *Standard* condition and the *Noisy* condition. There was no significant difference between these conditions ($mean_{Standard} = 4.6 \pm 0.08$ °/s $mean_{Noisy} = 4.7 \pm 0.07$ °/s; $P = .34$), suggesting that participants referred on average to the same velocity of reference movement in both conditions.

Data analysis

In order to evaluate and compare participants' perceptual performance across the three stimulation conditions (T, V, VT), the psychometric data (i.e. the proportion of "faster than the reference" answers at different stimulation intensities) were fitted by a cumulative Gaussian function:

$$P(x) = \lambda + (1 - 2\lambda)\frac{1}{\sigma_\Psi\sqrt{2\pi}}\int_{-\infty}^{x} e^{-\frac{(y-\mu_\Psi)^2}{2\sigma_\Psi^2}}\,dy$$

where x represents the stimulus velocity (in degrees per second); μ_ψ is the mean of the Gaussian, i.e. the Point of Subjective Equality (PSE) that corresponds to the stimulation intensity leading the participant to perceive an illusory movement on average as fast as the reference set at 5 °/s; σ_ψ is the standard deviation of the curve, or discrimination threshold, which is inversely related to the participant's discrimination sensitivity. In other words, a smaller σ_ψ value corresponds to a higher sensitivity in the discrimination task. The two indices, PSE and σ_ψ, characterize the participant's

255 performance. λ accounts for stimulus-independent errors due to participant's lapses and was restricted
256 to small values ($0 < \lambda < 0.06$, Wichmann and Hill, 2001), This parameter is not informative about the
257 perceptual decision, thus we disregarded it for the following analyses. Psignifit toolbox implemented
258 on Matlab software (© 1994-2014 The MathWorks, Inc.) was used to fit the psychometric curves
259 (Wichmann and Hill, 2001).

260 To compare discrimination sensitivity across the three stimulation conditions (T, V and VT),
261 we performed a one-way repeated-measures ANOVA with Tukey post-hoc tests on σ_ψ values. In
262 addition, for each participant, the enhancement of the visuo-tactile discrimination sensitivity over the
263 best unisensory one was assessed using the multisensory index (MSI) as defined by (Stein et al., 2009).
264 Since an improvement of discrimination sensitivity corresponded to a decrease in σ value, the MSI was
265 computed as follows:

266 $$MSI\ (\sigma_\psi) = \frac{Min(\sigma_{\psi T}; \sigma_{\psi V}) - \sigma_{\psi VT}}{Min(\sigma_{\psi T}; \sigma_{\psi V})}$$

267 To quantify the perceptual strength of the illusions, the gain of the responses in the different
268 stimulation conditions was assessed as follow (in percentage):

269 $$Gain = \frac{Vref}{PSE} * 100$$

270 with the reference velocity V_{ref} set at 5 °/s.

271

272 For the fifteen participants, we compared the response gains between the three sensory stimuli (T,
273 V and VT) using a one-way repeated-measure ANOVA with Tukey post-hoc tests. For the thirteen
274 participants that underwent the *Noisy* condition, a two-way repeated-measure ANOVA was also
275 performed on the illusion gains to test the effect of the sensory stimulation (T, V and VT) and the
276 experimental condition (*Standard* vs *Noisy*).

277 The enhancement or depression of the visuo-tactile response gain over the best unisensory
278 response gain was computed using the multisensory index (MSI) as defined by (Stein et al., 2009)

$$MSI\ (Gain) = \frac{Gain_{VT} - Max(Gain_T; Gain_V)}{Gain_{VT}} * 100$$

Models

The Maximum Likelihood Estimate model used to predict optimal multimodal discrimination performance

Insert Figure 2 around here

As illustrated in Figure 2, the minimum-variance linear combination model (often referred to as Maximum Likelihood Estimate (MLE) model) predicts how an "optimal observer" would combine two unbiased sensory signals to optimize the resulting perception (in the sense of minimizing its variance) relative to the two unimodal representations. According to MLE rules (which are just one particular instantiation of the more general Bayesian framework, see Landy et al. 2011), the optimal perceptual estimate in visuo-tactile stimulation can be described by the normalized product of the unimodal Likelihood distributions $P(\vartheta_T|\vartheta)$ and $P(\vartheta_V|\vartheta)$, with the underlying assumption that visual and tactile sources are conditionally independent variables affected by Gaussian noise:

$$P(\vartheta_{VT}|\vartheta) \propto P(\vartheta_T|\vartheta) * P(\vartheta_V|\vartheta) \quad (1)$$

where ϑ_T , ϑ_V and ϑ_{VT} are the tactile, visual and visuo-tactile estimates of hand velocity for a given value of stimulation velocity ϑ.

The visuo-tactile Likelihood resulting from the normalized multiplication of the two unimodal Gaussians is a Gaussian distribution itself, with a variance $\sigma^2{}_{VT}$ related to the unimodal variances through the following equation

$$\frac{1}{\sigma^2{}_{VT}} = \frac{1}{\sigma^2{}_V} + \frac{1}{\sigma^2{}_T} \quad (2)$$

303 Therefore, equation 2 implies that if the two sensory signals are optimally integrated, the visuo-tactile
304 variance is smaller than the variance of either modality in isolation, thus leading to a sensitivity
305 enhancement.
306 The MLE model and its predictions can easily be tested on the behavioral data of a multisensory
307 discrimination experiment. It can be shown that the same relation presented in equation 2 for the
308 variance of the sensory likelihood does actually apply to the standard deviation (σ_ψ) of the estimated
309 cumulative-Gaussian psychometric curve (i.e. its discrimination threshold). In particular, in this study,
310 predicted and observed visuo-tactile discrimination thresholds were compared in order to determine if
311 the integration of vision and touch was optimal with regard to the discriminative sensitivity of the
312 participants.
313 It should be noticed that in the present experimental context, the uncertainty related to the reference
314 movement velocity estimation could account for a portion of the estimated discrimination threshold σ_ψ.
315 We will address this issue in the next session.
316
317 *A Bayesian model to account for the low-perceptual gain of movement illusions*
318 In the present study, kinesthetic illusions of hand movements were induced while participants were
319 aware that their hand was actually not moving. This Prior knowledge was also supported by muscle
320 proprioceptive feedback from their stationary wrist. The conflict between this static information and
321 the moving tactile or visual information may account for the extremely low gain of the velocity
322 illusions with respect to the actual velocity of the moving stimuli (Blanchard et al., 2013).
323 In order to account for the low gain of the uni- and multimodal illusions, a more complex Bayesian
324 model was elaborated including a zero-centered Gaussian Likelihood accounting for muscle
325 proprioceptive cues and a Gaussian Prior distribution centered on zero too. The combination of those
326 two distributions is also a zero-centered Gaussian distribution. Therefore, to preserve the model
327 parsimony, we will treat these distinct contributions as a single probability distribution and we will
328 refer to it as “Prior” throughout the present manuscript.

The sensory Likelihood and the Prior distributions are combined according to Bayes' rule to obtain the Posterior distribution:

$$P(\vartheta|\vartheta_i) \propto P(\vartheta_i|\vartheta) * P(\vartheta) \quad (3)$$

with $P(\vartheta)$ = Prior probability distribution of hand velocity, $P(\vartheta_i|\vartheta)$ = sensory Likelihood for the modality i, and i = T,V or VT.

The parameters (mean and variance) of the Bayesian Gaussian distributions are linked by the following relations:

$$\begin{cases} \frac{\mu_{Post_i}}{\sigma^2_{Post_i}} = \frac{\mu_i}{\sigma^2_i} + \frac{\mu_{prior}}{\sigma^2_{Prior}} \\ \frac{1}{\sigma^2_{Post_i}} = \frac{1}{\sigma^2_i} + \frac{1}{\sigma^2_{Prior}} \end{cases} \quad (4)$$

with i = T, V or VT, μ_{Prior} = 0 °/s, σ^2_{Prior} is the unknown variance of the Prior (assumed to be constant throughout the different experimental conditions), μ_i the mean of the Likelihood, σ^2_i the unknown variance of the Likelihood and, similarly, μ_{Post_i} and $\sigma^2_{Post_i}$ are the mean and variance of the Posterior distribution. In line with most Bayesian models, we assumed that the Likelihood mean exactly matches the velocity stimulation ($\mu_i = \vartheta_i$) as it represents the first stage of (presumably unbiased) sensory encoding of global motion information. We also assumed that σ^2_i does not depend on velocity in the considered range. Although this last assumption is probably not true in general (e.g. Stocker & Simoncelli 2006), it seems to be a reasonable approximation for the relatively small range of stimulation velocities considered here.

Given all the above-mentioned assumptions, the estimated parameters of the psychometric function can be put in relation to the parameters of the hidden Bayesian distributions. A Bayesian ideal observer uses the information provided by the Posterior distribution to formulate a perceptual judgment, such as the velocity discrimination in our study. As shown in Figure 3, the proportion of judgments of the type

"*test faster than reference*" is equal to the integral of the Posterior distribution over the interval $]V_{ref}: +\infty[$

Insert Figure 3 around here

Let us consider two values of the stimulation velocity that correspond to the critical parameters of the psychometric curve, namely the PSE and the value at which $\Psi = 0.84$ which corresponds by definition to (PSE+σ_Ψ).

When the test velocity $\vartheta_i = PSE$ the ideal observer perceives on average by definition a velocity equivalent to the reference velocity V_{ref}. Thus the mean (and most likely value) of the Posterior distribution μ_{Post} is equal to V_{ref}.

On the other hand, when the test velocity is $\vartheta_i = PSE + \sigma_\Psi$, the integral under the Posterior is 0.84, which - on the ground of the assumption of normality - implies that its mean μ_{Post} is equal to ($V_{ref} + \sigma_{post}$).

By substituting these equalities in the system of equations 4, we obtained the expression of the variance of the three Bayesian distributions as a function of the parameters of the psychometric curve (PSE_i, σ_i) and of V_{ref}.

(5) $$\frac{1}{{\sigma^2}_i} = \frac{PSE_i}{V_{ref}} * \frac{1}{{\sigma^2}_{\Psi i}}$$

(6) $$\frac{1}{{\sigma^2}_{Prior}} = \frac{PSE_i}{V_{ref}} * \frac{1}{{\sigma^2}_{\Psi i}} * (\frac{PSE_i}{V_{ref}} - 1)$$

(7) $$\frac{1}{{\sigma^2}_{Post}} = \frac{{PSE_i}^2}{{V_{ref}}^2} * \frac{1}{{\sigma^2}_{\Psi i}}$$

374 Note that these equations hold for each type of stimulation (T, V or VT). The variance of the Prior
375 distribution was thus estimated (through Equation 6) for each of the unimodal conditions V and T.
376 Consistent with our assumption of a constant Gaussian Prior noise across experimental conditions, we
377 verified that the σ_{Prior} estimated by the "tactile" and the "visual" equation (6) did not differ
378 significantly (Student's paired *t*-test: $P = .063$). We used the mean of the Prior variance estimated from
379 the visual and tactile psychometric parameters (Equation 6) for the later steps (see also Fig. 4; Step 1).
380 We then applied the MLE predictions for the estimate of the Likelihood variance in the condition of
381 visuo-tactile stimulation (Equation 2) and then inverted the Equations 5, 6 and 7, relating the Bayesian
382 to the psychometric parameters, in order to predict the bimodal point of subjective equality PSE_{VT}
383 (Fig. 4; Step 2),

384 (8) $$PSE_{VT}^{pred} = V_{ref} * \left(1 + \frac{\sigma^2{}_{VT}}{\sigma^2{}_{Prior}}\right)$$

385 where both σ_{VT}^2 and σ_{Prior}^2 can be expressed as functions of the unimodal psychometric parameters.
386 For all participants, the predicted gain G_{VT} of the visuo-tactile illusion in the *Standard* condition could
387 finally be compared to the observed visuo-tactile gain.
388 As previously pointed out, the uncertainty related to the estimation of the reference movement velocity
389 could account for a portion of the perceptual variability in our hand-velocity discrimination task,
390 whatever the sensory stimulation. Therefore we assessed its influence by including the individual
391 variability of the reference movement reproduction (see Methods section) in the estimation of the
392 global uncertainty for the velocity discrimination task. However, doing so increased the complexity of
393 the model without improving the predictions, nor changing the core results. For the sake of parsimony,
394 we will only briefly present the impact of this additional component of perceptual uncertainty on the
395 predictions at the end of the Result section.
396
397 In addition, the same analysis was performed on perceptual responses elicited in the *Noisy*
398 condition, where co-vibration was applied onto antagonist wrist muscles to disturb static muscle

proprioceptive feedback. The variance of the Prior σ^2_{Prior} in the *Noisy* condition was estimated and the visuo-tactile illusion gain G_{VT} was predicted.

The relative contribution of the Prior in the final perception was also assessed by computing the relative weight of the Prior with respect to the visual and tactile weights, as follows:

$$\omega_{Prior} = \frac{\sigma_{Prior}^{-2}}{\sigma_{Prior}^{-2} + \sigma_T^{-2} + \sigma_V^{-2}}$$

The relative weights of the Prior obtained in *Standard* and *Noisy* conditions were compared using a Student's paired t-test.

Finally, to test whether the model better fit the visuo-tactile performances in the *Noisy* condition compared to the *Standard* condition, the differences between predicted and observed gains in the two conditions were compared using a Student's paired t-test.

Insert Figure 4 around here

Results

Discriminative ability for hand movement velocity based on visual and/or tactile inputs

As expected, for all the participants included in the study, the counterclockwise rotation of the visual and/or tactile stimulation gave rise to an illusory sensation of rotation of their stimulated hand, which was always oriented in the opposite direction, i.e. clockwise. For each stimulation condition (T, V, VT) randomly applied at six different velocities, participants reported whether the illusion was faster or slower than the 5 °/s clockwise reference rotation they actively performed just before or just after the stimulation delivery. To compare the participants' performance in the velocity discrimination task between tactile, visual, and visuo-tactile stimulation, the probability of perceiving the illusion as faster than the reference movement was fitted by a cumulative Gaussian function for the tested stimulus velocities to obtain three individual psychometric curves.

As shown in the example of Figure 5A, the participant experienced an illusory movement with a velocity close to the 5 °/s reference when the tactile or the visual stimulation was rotating around 29.8 °/s and 28.8 °/s, respectively. The participant's ability to discriminate the velocity of his/her hand movement improved in the visuo-tactile condition compared to the unimodal ones, as attested by an increased slope of the visuo-tactile psychometric curve. More precisely, the discrimination threshold σ (i.e. the increase in stimulation velocity required to induce an illusory movement faster than the reference movement in 84 % of the trials with respect to 50 % of the trials) was lower in the visuo-tactile condition (mean σ_{VT} = 6.02 ± 2.19 °/s) than in the unimodal conditions (mean σ_T = 8.67 ± 3.6 °/s; mean σ_V = 7.68 ± 3.5 °/s). In other words, the decrease in σ value reflected the fact that the velocity discrimination ability of this participant increased in the visuo-tactile condition.

These individual results were confirmed at the group level (Fig. 5B). Performances in velocity discrimination changed according to the stimulation condition ($F(2, 28) = 12.375$, $P = .00014$). The mean σ decreased significantly in the visuo-tactile condition in comparison with the tactile (post-hoc test: $P < .001$) and visual conditions (post-hoc test: $P = .0025$). Discrimination thresholds for the velocity discrimination task did not significantly differ between the two unimodal conditions ($P = .58$).

In order to quantify the benefit resulting from visuo-tactile stimulation, the multisensory index (MSI) was calculated individually for the σ values. This index, expressed in percentage, reveals for each participant the enhancement (or depression) of the multisensory sensitivity over the best unisensory response (Stein et al., 2009). For eleven of the thirteen participants, the multisensory response showed a positive benefit on the discriminative threshold σ. Quantitatively, the visuo-tactile σ values for those eleven participants were lower than the lowest of the unimodal σ, with an MSI ranging between 3 % and 40 % (Fig. 5C). Only two among 15 participants did not show an improvement of their discriminative sensibility in the visuo-tactile condition.

As depicted in Figure 2, the MLE model predicts an improved discrimination performance in the multimodal condition. The MLE-predicted visuo-tactile σ values were estimated for each participant on the basis of his/her performances in the two unimodal conditions. As illustrated in Figure 5D, comparing these estimates to the experimental observations during the visuo-tactile condition showed that the data estimates did not differ significantly from the observed σ values (Student's Paired *t* test, *P* = .55). Note that including the variability of the reference reproduction task in the model did not change the predictions of the discriminative thresholds in any appreciable way (0.9 % of difference in the worst case…).

Insert Figure 5 around here

A low-perceptual gain for movement illusions

Standard condition

In the individual results presented in Figure 6A, illusory movement was perceived at a velocity close to the 5 °/s reference when the tactile or the visual stimulation was rotating at about 29 °/s, with a point of subjective equality (PSE) estimated at 28.8 and 29.8 °/s, respectively. When the two kinds of stimulation were combined, the velocity of the stimulation required to evoke an illusion close to the 5 °/s reference dropped to 20.5 °/s (Fig. 6A). The decrease in PSE reflected the fact that the participant perceived a faster illusory movement with combined visual and tactile stimulation compared to only one kind of stimulation. These results can also be expressed in terms of response gain, classically defined as the ratio between the perceived illusion velocity and the actual velocity of the stimulus (see Method section). A value of 100 % would indicate that the participant perceived a hand movement at the same velocity as the actual stimulation velocity. In our experimental paradigm, the gains of the illusions were always much lower than 100 %. They were on average about 19.9 % (± 2.7 % SD) and 18.4 % (± 2.9 % SD) for the tactile and visual stimulation, respectively. During visuo-tactile

stimulation, the gain significantly increased, up to 23.7 % (± 3.5 % SD) in comparison with unimodal tactile (post-hoc test: $P = .0004$) and visual (post-hoc test: $P < .0001$) stimulations: illusion velocity got closer to the actual stimulation velocity in visuo-tactile condition (Fig. 6B). A more detailed analysis showed that the multimodal gain increased for all participants except one (Fig. 6C). This increase was also attested by positive MSI values, ranging from 1 % to 40 % for 14 of the 15 participants (mean MSI = 14 % ± 13).

Insert Figure 6 around here

To account for these low-perceptual gains, we then considered a more complex model than the MLE, including the influence of the "non-moving hand information" *a priori* present in our experimental paradigm. Indeed, in addition to the omnipresent proprioceptive static cue, participants were always aware that their hands were not actually moving. By modeling the "non-moving hand information" as a Gaussian distribution centered on zero, the variance of this Prior was first estimated through the observed data obtained in the two unimodal conditions (Fig. 3 & 4 Step 1). In line with our assumption that the Prior distribution should be constant over the various sensory conditions, we found that the variance estimates based on each single sensory performance did not differ significantly ($P = .18$).
The visuo-tactile Likelihood was then predicted by combining the estimated Prior distribution with the estimated unisensory Likelihoods (see Fig. 3 & 4 Step 2).
This model predicted that the gain of the illusion in the visuo-tactile condition would improve compared to the unimodal ones. However, the observed increase in gain was less than that predicted by the model (Fig. 6D). By taking into account the variability of the reference movement perception in the model, predictions were not improved (they became actually worse, in the worst case, discrepancies between observations and predictions of the gain went from 3.9 % to 9.8 %), but the discrepancy between data and model predictions did not qualitatively change, highlighting in all cases an overestimation of the gain increase by the Bayesian complete model.

Noisy condition

To further explore the influence of the "non-moving hand" cues in our paradigm, the same experiment was performed while muscle proprioception was disturbed by equivalent vibrations applied on antagonist wrist muscles involved in left-right hand movement: the right *pollicis longus* and *carpi ulnaris extensor* muscles. Applied on antagonist muscles with the same low frequency, mechanical vibration equally activates muscle spindle endings, masking natural muscle spindle afferents without giving rise to any relevant movement information (Roll et al., 1989; Calvin-Figuière et al., 1999). Before the beginning of each experimental session, we ensured that muscle co-vibration did not induce any movement sensation.

During co-vibration, all the participants were still able to experience the illusory movement elicited by the tactile and/or visual stimulation. In the *Noisy* condition, the stimulus velocity required for the illusory movement to reach a velocity close to the reference value was lower than that previously observed in the *Standard* condition where no vibration was applied. A two-way ANOVA analysis showed that the gains of the perceptual illusions increased significantly in the *Noisy* conditions compared to the *Standard* ones (Main effect of condition ($F(1, 12) = 26.003$; $P = .00026$). When the two *Noisy* and *Standard* conditions were confounded, the gain observed in the visuo-tactile conditions was significantly higher than those observed in the tactile and visual conditions ($F(2, 24) = 25.37$; $P < .0001$) (Fig.7). No significant interactions were found between the condition (*Noisy* vs S*tandard*) and stimulation (T, V, VT) factors.

Insert Figure 7 around here

As in the previous *Standard* experiment, we estimated the variance of the Prior based on unimodal responses collected during co-vibration. With degraded muscle proprioceptive information, the influence of the "non moving hand" information modeled by the Prior was supposed to be reduced in the *Noisy* conditions. As expected, for the 13 participants tested, the relative weight of the Prior

(compared to the tactile and visual relative weight) was lower in the *Noisy* experiment (0.89 ± 0.03) than in the *Standard* one (0.95 ± 0.017; Student's paired *t* test: $P = .011$).

In addition, the predicted gains of the visuo-tactile responses were estimated on the basis of the unimodal and Prior distributions obtained with concomitant co-vibration. Although the predicted gains were still higher than those observed experimentally, the discrepancy between data and model predictions was reduced in the *Noisy* experiment with respect to the *Standard* one (Student's paired *t* test: $P = .019$; see Figure 8).

Insert Figure 8 around here

Discussion

Optimal visuo-tactile integration in velocity discrimination of self-hand movements

The present study shows that visual and tactile motion cues can be equivalently used by the CNS (central nervous system) to discriminate the velocity of self-hand movements. By combining both types of stimulation at the same velocity, one can assume that we generated congruent multisensory signals, as during actual hand movements. As expected, we observed a multimodal benefit provided by the combination of visual and tactile motion cues when participants evaluated the velocity of self-hand illusion rotation. This behavioral improvement was first of all attested by a better discrimination ability (a lower discrimination threshold) in bimodal than in unimodal conditions.

The perceptual benefit of combined vision and touch had mainly been estimated when one has to assess properties of an external objet like its size (Ernst and Banks, 2002) or its speed (Bensmaia et al., 2006; Gori et al., 2011). In those studies, as in the present one, the multimodal benefit is well predicted by the MLE principle suggesting that vision and touch are combined in an optimal way when discriminating perceived self-hand velocity.

Moreover, participants' ability to discriminate the velocity of an illusory hand movement was equivalent when based on the rotation of either the tactile disk or the visual background with a

549 discrimination threshold about 8 °/s for both conditions. This is consistent with the study by Gori et al.
550 (2011) showing equal sensitivities to discriminate the velocity of external motion signals of tactile or
551 visual origin. One can thus hypothesize that common inferential processes take place in situations of
552 visuo-tactile integration in the context of velocity discrimination, whether the perceived object is the
553 self or an external object.

554 ***Influence of the non-moving hand Prior in the low-perceptual gain of movement illusions***

555 A strong difference emerges for the absolute estimation of the velocity depending on whether
556 visual and tactile motion signals are related to an external object or to self-body. Whereas velocity
557 estimation of a tactile stream on a fingertip is close to the actual velocity of the moving object
558 (Bensmaia et al., 2006), velocity of the perceived self-hand movement in the present experiment was
559 drastically underestimated with a perceived movement speed always lower than 30 % of the actual
560 visual or tactile stimulation velocity. One plausible explanation is that since proprioceptive afferents
561 from participants' wrist muscles informed the CNS that the hand was not actually moving, the sensory
562 conflict might have resulted in a slower perception of hand rotation. To account for this unavoidable
563 proprioceptive feedback together with the fact that participants knew that their hand was actually not
564 moving, we developed a Bayesian model including a Prior term defined as the product of two
565 Gaussian distributions (the Proprioceptive static sensory Likelihood and the cognitive Prior) centered
566 on zero. We postulated that, when visual or tactile stimulation was applied, the final perception of
567 illusory hand movement resulted from the combination of the visual, tactile or visuo-tactile motion
568 cues with this zero-centered Prior. Our parameter-free Bayesian model successfully predicted a gain
569 increase in visuo-tactile illusions compared to unimodal ones. In the Bayesian framework this effect is
570 explained by the stronger weight of the sensory information when two modalities are optimally
571 combined and hence reliability is increased. In a self-angular displacement estimation task, Jürgens
572 and Becker (2006) had postulated a Prior favoring a particular rotation speed to account for the
573 velocity-dependent bias observed in the participants judgments. Albeit that study did not test a
574 quantitative prediction on the observed bias reduction in multisensory stimulation, the authors'

conclusions are consistent with ours and point to a probabilistic integration of sensory representations with a prior knowledge as postulated by Bayes theory. However, the observed gain increase in the present experiment did not match the predicted values, which were over-estimated. In the following section we discuss some possible explanations.

Suboptimal multisensory integration: insights into the underlying mechanisms

Deviations from optimal integration predictions have already been reported in cases of sensory conflicts, when sensory information is strongly non-coherent across different modalities. Suboptimal cue weights have been reported in conflictual situations where visual and vestibular inputs are manipulated to give incongruent spatial information relative to passively imposed body rotations (Prsa et al., 2012). In the latter case, participants over-weighted the visual cues to discriminate the angle of imposed rotations. Conversely, vestibular cues were found excessively preponderant to visual cues in a heading perception task (Fetsch et al., 2009).

In the present experiment, several explanations may account for the suboptimal benefit on the perceptual gain for visuo-tactile stimulation.

First, it has been shown that in case of extreme conflict, integration can be prevented, favoring segregation of the multisensory information (Bresciani et al., 2004; Roach et al., 2006; Körding et al., 2007; van Dam et al., 2014). Accordingly, causal inference models predict a variable degree of multisensory integration according to the probability of the incoming signals to be causally related to a common origin in the world (Körding et al., 2007). In the present study, one can speculate that, if the statistical inference process assigns high weight to a single cause (proprioception, vision and touch all originating from the same true source), then one would indeed find a strengthening of the illusion when a second moving cue is added to the first one. On the other hand, having two moving sensory cues instead of one may increase the conflict between static and movement information, thus leading to a lower weight for the common origin hypothesis. In the latter case, this conflict increase may have degraded multisensory integration and may then have led the participants to partly attribute the visual

and tactile motion cues to a different origin, in the environment, rather than their own body. However, a change in causal attribution does not seem to fully explain the present results since it is not consistent with the observation of an increased (although suboptimal) gain in the visuo-tactile condition and also the fact that all the participants reported more salient illusory hand movements in bimodal compared to unimodal conditions. Lastly, segregation is more likely to occur for large discrepancies between cues. Therefore future studies should be conducted to test whether increasing the conflict between static and motion information (using higher velocity stimulation) results in a greater deviation from optimality.

Regardless of the conflict between static and motion cues, a second explanation for the overestimation of the bimodal gain improvement can be considered. One can speculate that there is an illusory percept that is being used for a behavioral report and simultaneously a non-reported judgment of background motion and those may interact. In this context, combining visual and tactile cues leads to a decrease in the variability of the velocity estimate, both for self-body movements (as suggested by our psychophysical results) and for external object motions (Gori et al, 2011). As a consequence, if participants have a more coherent percept of the rotation of the environment under their hand, this should in turn facilitate the attribution of the movement to the environment rather than to the hand during the bimodal condition compared to the unimodal conditions, and finally result in sub-optimal performances as compared to Bayesian predictions. Nevertheless, this argument alone fails to explain the observed improvement of gain predictions in the *Noisy* condition. Indeed, muscle proprioceptive noise should not have affected the way external object motion was perceived.

Finally, taking into account the crucial role of muscle proprioception in kinesthesia, the suboptimality in the present study can be interpreted as a weighting bias in favor of this modality. Biases toward one sensory cue in multisensory conflicting situations that cannot be explained by a Bayesian weighting process can rather be attributed to a recalibration mechanism (Adams et al., 2001; Block and Bastian, 2011; Wozny and Shams, 2011; Prsa et al., 2012). To solve the discrepancy between two sensory estimates, the brain may choose to realign all the sensory estimates with respect to the most appropriate one. This interpretation is consistent with the *appropriateness principle* (Welch

et al., 1980): discrepancies between senses tend to be resolved in favor of the modality not only generally more reliable, but also more appropriate to the task at hand. Recently, Block and Bastian (2011) demonstrated that the weighting and realigning strategies are two independent processes that might occur in conjunction.

In the present experiment, the conflict increase between static and movement information may lead to an apparent suboptimal estimation of the illusion velocity due to a recalibration of the visuo-tactile estimation with respect to the static proprioceptive information. Indeed, the CNS may rely more on less ambiguous information, which is muscle proprioceptive information, rather than on visual or tactile information which can both relate to either self-body or environmental changes. Such a recalibration mechanism could thus explain why the perceptual benefit of the bimodal situation was lower than predicted.

To test this hypothesis, we degraded muscle proprioceptive signals in order to reduce the reliability of the static information. Natural messages from muscle spindles were masked thanks to a concomitant vibration applied onto the wrist antagonist muscles (Roll et al., 1989). Such vibration efficiently degraded the information of hand immobility: the velocity required to give rise to an illusory movement with a velocity close to the reference value was lower than previously observed in the *Standard* condition (with no vibration). In other words, the same visual or tactile stimulation gave rise to faster illusory movements when muscle proprioception was masked by the vibration. Using the mirror paradigm, Guerraz et al. (2012) consistently reported that the illusory movement sensation of one arm evoked by the reflection on a mirror of the contralateral moving arm increased with a proprioceptive masking of the arm subjected to kinesthetic illusion.

As expected, the proprioceptive noise enabled our model to better fit the observed illusion gains. However, the model predictions still over-estimated the visuo-tactile benefit on gain, suggesting that attenuating muscle proprioceptive feedback was not sufficient. This quantitative discrepancy may be due to incomplete masking of proprioceptive afferents through our non-invasive stimulation. In addition, static information cannot be completely cancelled, since the participants were always aware

653 that no actual hand movement was occurring during the experiment. This cognitive component might
654 have pushed towards a sensory realignment in conjunction with a greater muscular proprioception
655 reweighting in the visuo-tactile estimation of illusory hand movements.
656
657 ***Physiological evidence for visuo-tactile integration and Bayesian inferences***
658 A large number of studies performed in animals and humans have recently provided compelling
659 evidence for the neural substrates of multisensory integrative processing, including in the early stages of sensory
660 information processing (for reviews see Cappe et al., 2009; Klemen and Chambers, 2012). Bimodal neurons
661 sensitive to both visual and tactile stimuli applied on the hand have been found in the premotor and parietal
662 areas of the monkey (Graziano & Gross, 1998; Grefkes & Fink, 2005), when spatially congruent stimuli from
663 different origins are simultaneously presented to the animal. Neuroimaging studies further support that
664 heteromodal brain regions are specifically activated in the presence of different sensory inputs (Calvert, 2001;
665 Downar et al., 2000; Gentile et al., 2011; Kavounoudias et al., 2008; Macaluso & Driver, 2001). By applying
666 coincident visual and tactile stimuli on human hands, Gentile et al. (2011) used fMRI to show the involvement
667 of the premotor cortex and intraparietal sulcus in visuo-tactile integration processing, supporting observations
668 previously reported in monkeys. More generally, the inferior parietal cortex has been found to subserve visuo-
669 tactile integrative processing for object motion coding in peripersonal space (Bremmer et al., 2001; Grefkes and
670 Fink, 2005) as well as for coding self-body awareness (Kammers et al., 2009; Tsakiris, 2010).
671 Interestingly, direct or indirect interactions between primary sensory areas have been recently evidenced
672 (Ghazanfar & Schroeder, 2006; Cappe et al., 2009). Recently, using an elegant design inspired by the Bayesian
673 framework, Helbig et al. (2012) showed that during a task of shape identification, activation of the primary
674 somatosensory cortex can be modulated by the reliability of visual information within congruent visuo-tactile
675 inputs. The more reliable the visual information, the less activity in S1 increased.
676 Meanwhile, computational modelling approaches have demonstrated that a simple linear summation of neural
677 population activity may account for optimal Bayesian computations (Knill & Pouget, 2004; Ma et al., 2006;
678 Fetsch et al., 2013). By recording single neurones sensitive to both vestibular and visual stimuli within the
679 dorsal medial superior temporal area (MSTd) in monkeys, a brain region activated during self-body motion,

Morgan et al. (2008) provided evidence for the neural basis of Bayesian computations in kinesthesia. During presentation of multisensory stimulation, MSTd neurones displayed responses that were well fit by a weighted linear sum of vestibular and visual unimodal responses.

Altogether these observations support the assumption that the level of activation of primary sensory regions may reflect the relative weight of the sensory cues, and that the perceptual enhancement due to convergent multisensory information might be achieved through a multistage integration processing involving dedicated heteromodal brain regions as well as direct interactions between primary sensory areas. Although the cerebral networks responsible for visuo-tactile integration involved in self-body movement perception remain to be identified, neural recordings from visuo-vestibular cortical regions support the assumption of a Bayesian-like multisensory integration at the cortical level, bridging the gap between neurophysiological, computational and behavioural approaches.

Conclusion

The present findings show for the first time that kinesthetic information from visual and tactile origins is optimally integrated to improve speed discriminative ability for self-hand movement perception. In addition, by inducing illusory movement sensations, we created an artificial conflict between static muscle proprioceptive information and moving tactile and/or visual information. Such sensory conflict might explain the low-perceptual gains of the observed illusions, as attested by the increase in illusion gain when muscle proprioception was masked. However, we observed an over-weighting in favor of the *non-moving hand cues* that cannot be fully predicted by a Bayesian optimal weighting process including a Prior favoring hand immobility. An additional recalibration strategy favoring the less ambiguous information in conflictual situations might explain such bias toward the static proprioceptive cues that are omnipresent and play a crucial rule for kinesthesia.

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Figure Captions

Figure 1: Experimental set-up and stimulation devices

A: Experimental set-up including stimulation devices and motion capture system (CODAmotion) to record actual right hand movements in the reference movement condition. B: Textured-disk used as tactile stimulation. C: Visual pattern displayed by a video projector (see A). D: Mechanical vibrators applied onto two antagonist wrist muscles (*pollicis longus* and *extensor carpi ulnaris*) to disturb muscle proprioceptive inputs (MP) in the *Noisy* condition

Participants exposed to a counterclockwise rotation of the tactile and/or visual stimuli had to report whether the induced clockwise illusion of hand rotation they perceived was faster or slower than the velocity of the reference movement they actively executed before or after each stimulation.

Figure 2: Schematic representation of the MLE principle

In order to estimate self-hand movement velocity, the CNS is supposed to proceed as an inference machine: following MLE rules, unisensory cues (noisy, normally-distributed representations of the stimulation velocity ϑ_T and ϑ_V on the basis of each sensory modality, touch and vision) are optimally combined to determine the minimum-variance visuo-tactile perceptual estimate ϑ_{VT}. The right panel illustrates the MLE prediction for the visuo-tactile Likelihood (with variance σ^2_{VT}, black curve) resulting from the optimal combination of unimodal Likelihoods (σ^2_T, σ^2_V, dark grey and light grey curves, respectively).

Figure 3: Relationship between Bayesian and psychometric functions

A and B represent two different relevant conditions of stimulations (1 and 2) used to determine the discriminative threshold: the PSE (A) and the intensity leading to 84.13 % of "faster than the reference velocity" answer (B). V_{ref} is the velocity of the reference movement (5 °/s). σ_{Post}, μ_{Post} and μ_i are

parameters of the Bayesian functions, respectively the standard deviation and mean of the Posterior distribution and the mean of the Likelihood function (assumed equal to the stimulation velocity). σ_Ψ and PSE are the psychophysical, measured parameters, respectively the variance and the mean of the psychometric function. We remind that the PSE is defined as the point of subjective equality, i.e. the stimulation intensity eliciting an illusory movement faster than the reference 50 % of the time. These relations allow to estimate all the parameters of the hidden Bayesian functions as a function of the psychometric parameters (see in Models).

Figure 4: Schematic representation of the key steps for predicting visuo-tactile gain on the basis of a Prior-equipped Bayesian model.

Step 1: Prior variability estimation: the standard deviation (σ_{Prior}) of the Prior distribution (black curve, centered on the null velocity) is estimated for each participant using (through Equation 6) the psychometric parameters estimated in unimodal visual (orange curves) and tactile (blue curves) conditions.

Step 2: Prediction of visuo-tactile gain: the expected PSE (Point of subjective equality) in visuo-tactile stimulation (mean of the visuo-tactile Likelihood depicted by the dashed green curve) is predicted on the basis of the estimate of the Prior variance (step 1), the MLE-estimate for σ^2_{VT} and Equation 7. The visuo-tactile gain is simply derived from the PSE (see definition in Method).

Figure 5: Comparison of velocity discrimination thresholds during tactile, visual and visuo-tactile stimulation

A. Extraction of σ from psychometric curves: Psychometric curves of one representative participant obtained by fitting the probabilities of perceiving the illusion as faster than the reference movement with a cumulative Gaussian distribution for the tactile stimulation (T, blue curve), visual stimulation

888 (V, yellow curve), and visuo-tactile stimulation (VT, green curve). The discrimination threshold, σ, is
889 the difference between the stimulation velocities leading to the «faster» answer 84.13 % of the times
890 and 50 % of the times, and it is inversely related to the slope of the psychometric function.
891 **B. Mean σ in bi- or unimodal stimulation**: Mean individual values of σ (grey bars) and mean (± SD)
892 values of σ extracted from the whole population data (N = 15) for tactile (blue square), visual (yellow
893 square), and visuo-tactile (green square) stimulation. For the mean σ values, significant differences
894 were found between the bimodal and each of the two unimodal conditions (* $P < .05$; ** $P < .01$).

895 **C. Multisensory Index for σ**: individual (grey bars) and mean Multisensory Index (MSI; green
896 square) for σ (N = 15 participants). Positive and negative values correspond respectively to a
897 multisensory benefit or loss in the discrimination performance of the participants with respect to their
898 most efficient unimodal performance.

899 **D. Comparison between observed and MLE-predicted σ**: Comparison between observed σ in visuo-
900 tactile stimulation and σ predicted by the MLE model for the 15 participants (S1 to S15). The green
901 diamonds correspond to the observed data and the error bars are the standard deviation. No significant
902 difference was found between predictions and observations of σ ($P = .55$, ns). Light green rectangles
903 represent 95 % CIs computed using the following bootstrap procedure. Choice data were resampled
904 across repetitions (with replacement) and refitted 1000 times to create sample-distributions of the
905 threshold for each psychometric function and for the predicted visuo-tactile parameters. The CIs were
906 directly estimated from these bootstrap-samples (percentile method).

907

908 **Figure 6: Comparison of the gains of the perceptual responses during tactile, visual and**
909 **visuo-tactile stimulation**

910 **A. Extraction of PSE from psychometric curves**: Psychometric curves of one participant obtained
911 by fitting the probability of perceiving the illusion as “faster than the reference” movement with a

cumulative Gaussian distribution for the tactile stimulation (T, blue curve), visual stimulation (V, yellow curve), and visuo-tactile stimulation (VT, green curve). The PSE (Point of Subjective Equality) corresponds to the stimulation velocity leading to the «faster than the reference» answer 50 % of the time.

B. Mean Gain in bi- or unimodal stimulation: Mean individual values of gain (grey bars) and mean (± SD) values of gain calculated as the ratio between the reference velocity, V_{ref}, and the actual velocity of the visual (yellow bars), tactile (blue bars) and visuo-tactile (green bars) stimulation at the PSE. For the mean gain values, significant differences were found between the bimodal and each of the two unimodal conditions (* $P < .05$; ** $P < .01$).

C. Multisensory Index for Gain: Individual (grey bars) and mean Multisensory Index (MSI; green square) of illusion gains (N=15 participants). Positive and negative values correspond respectively to a multisensory increase or decrease in the gain of the perceptual illusions of the participants with respect to the best unimodal performance.

D. Comparison between observed and Bayesian predicted Gain: Comparison between observed gain in visuo-tactile stimulation and gain predicted by the Bayesian model with a zero-centered Prior for the 15 participants (S1 to S15). The green diamonds correspond to the observed data and the error bars are the standard deviation. The increase of the bimodal gain was predicted but over-estimated by the model. Light green rectangles represent 95 % CIs computed using the following bootstrap procedure. Choice data were resampled across repetitions (with replacement) and refitted 1000 times to create sample-distributions of the threshold for each psychometric function and for the predicted visuo-tactile parameters. The CIs were directly estimated from these bootstrap-samples (percentile method).

936

937 **Figure 7: Comparison of illusion gains between *Standard* and *Noisy* conditions**

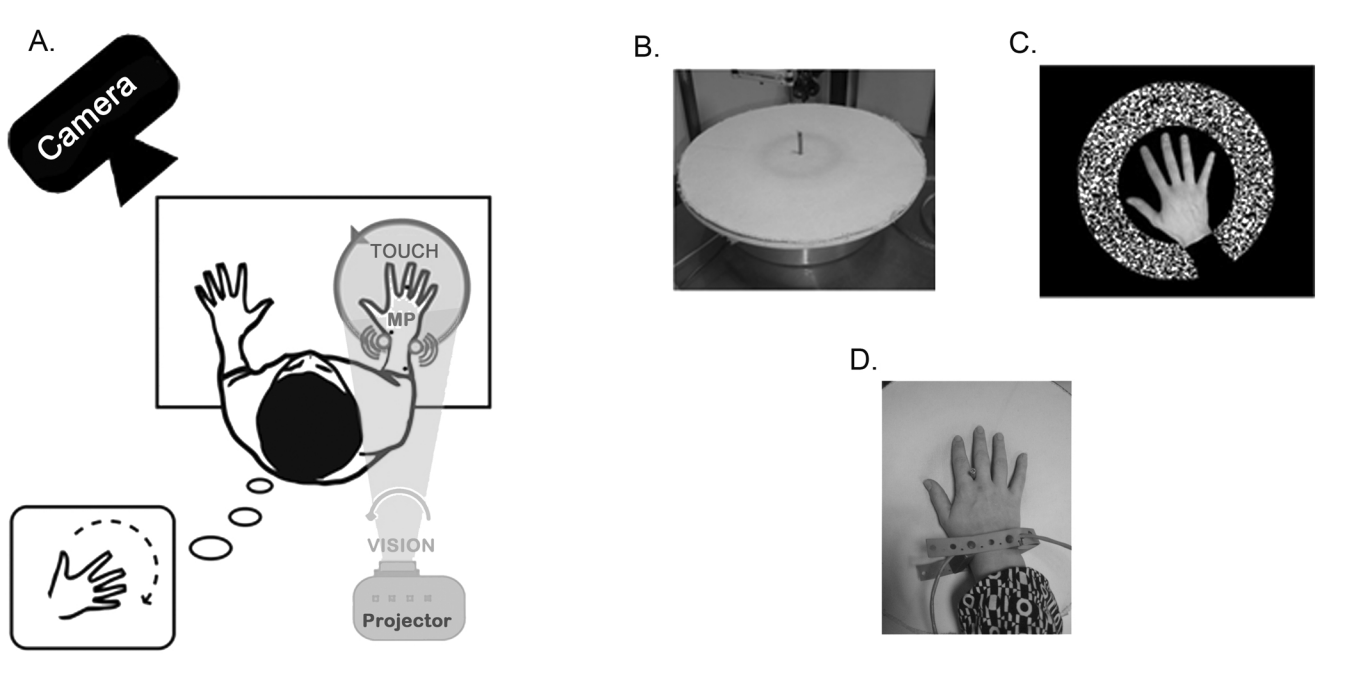
938 Mean gain (± SEM) of the discrimination responses induced by tactile (T, squares), visuo-tactile (VT,
939 triangles), and visual (V, diamonds) stimulation for the *Standard* (plain grey) and the *Noisy* (hatched
940 grey) conditions. Note that illusion gains observed in the *Noisy* conditions, in which muscle
941 proprioception afferents were masked by an ago-antagonist co-vibration, were significantly higher than
942 those in the *Standard* conditions whatever the stimulation (T, V, VT). * $P < .05$; ** $P < .01$

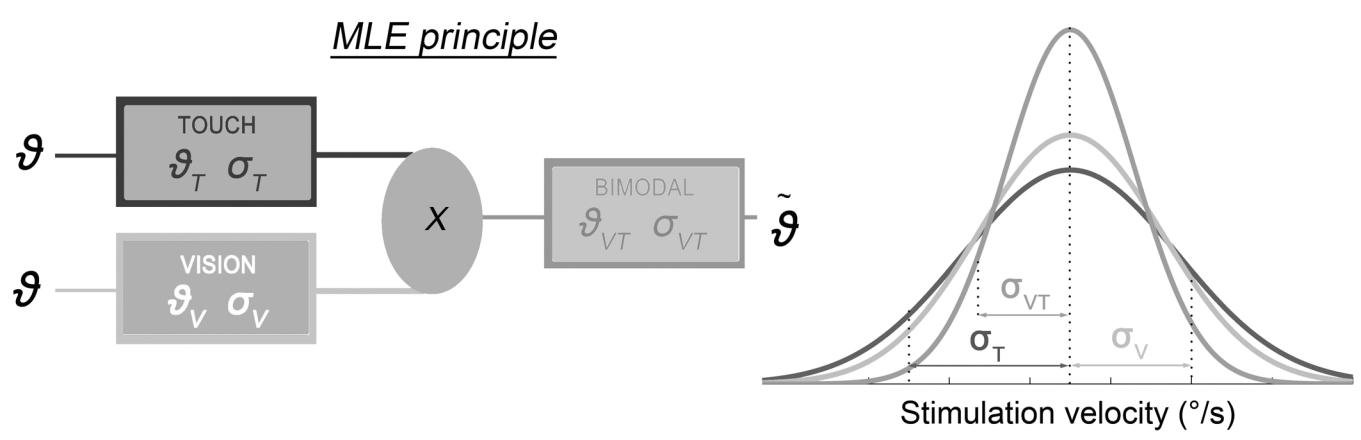
943

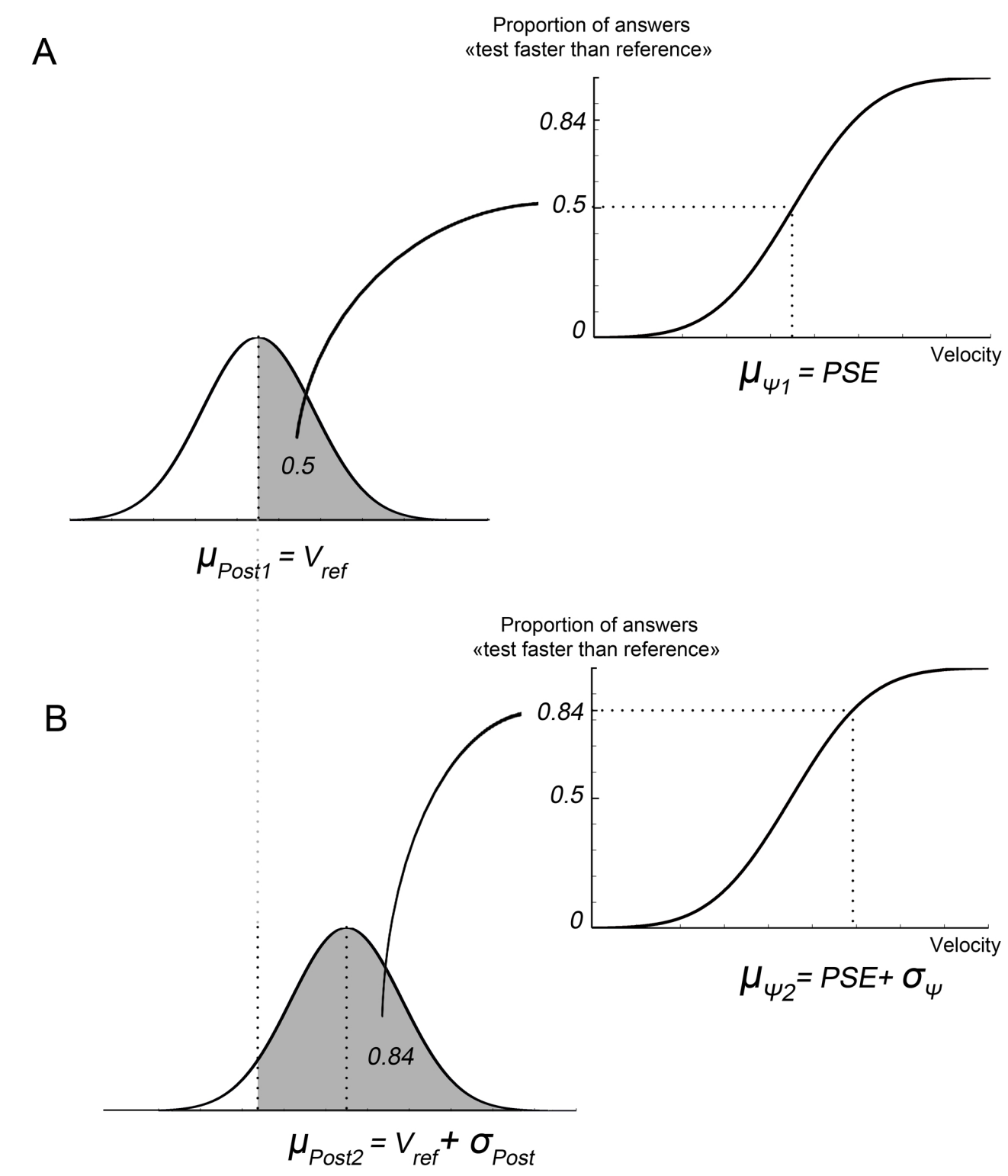
944 **Figure 8: Comparison of the Bayesian predictions for the *Standard* and *Noisy* conditions**

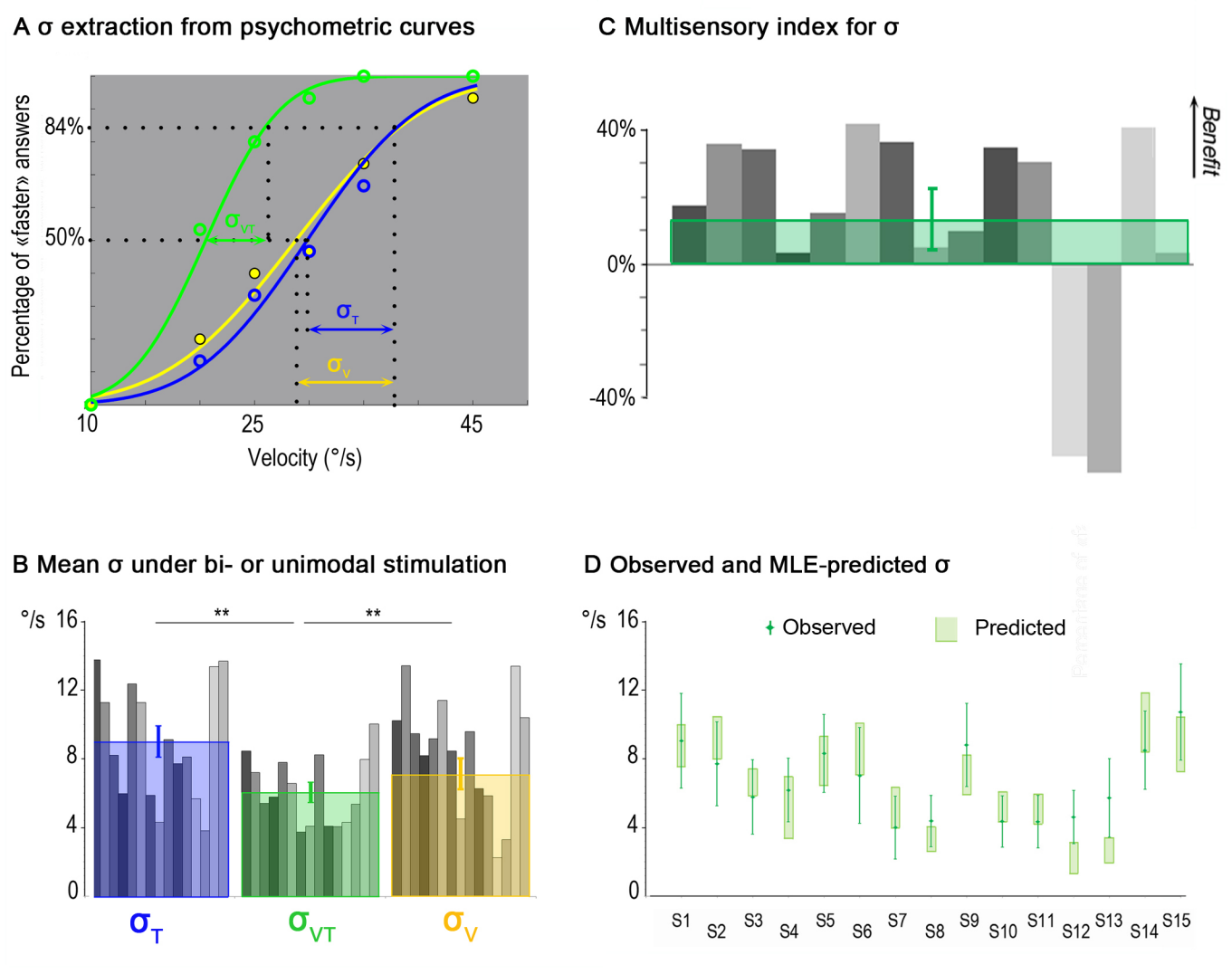
945 **A. Bayesian prediction vs observation in Noisy condition**: Comparison between observed gains in
946 visuo-tactile stimulation and gains predicted by the Bayesian model in the *Noisy* condition for the 13
947 participants (S1 to S13). The dots correspond to individual observed data and the error bars are the
948 standard deviation. represent 95 % CIs computed using the following bootstrap procedure. Choice data
949 were resampled across repetitions (with replacement) and refitted 1000 times to create sample-
950 distributions of the threshold for each psychometric function and for the predicted visuo-tactile
951 parameters. The CIs were directly estimated from these bootstrap-samples (percentile method).
952 Increase of the visuo-tactile gain was better predicted than in the *Standard* condition but remained
953 over-estimated by the model.

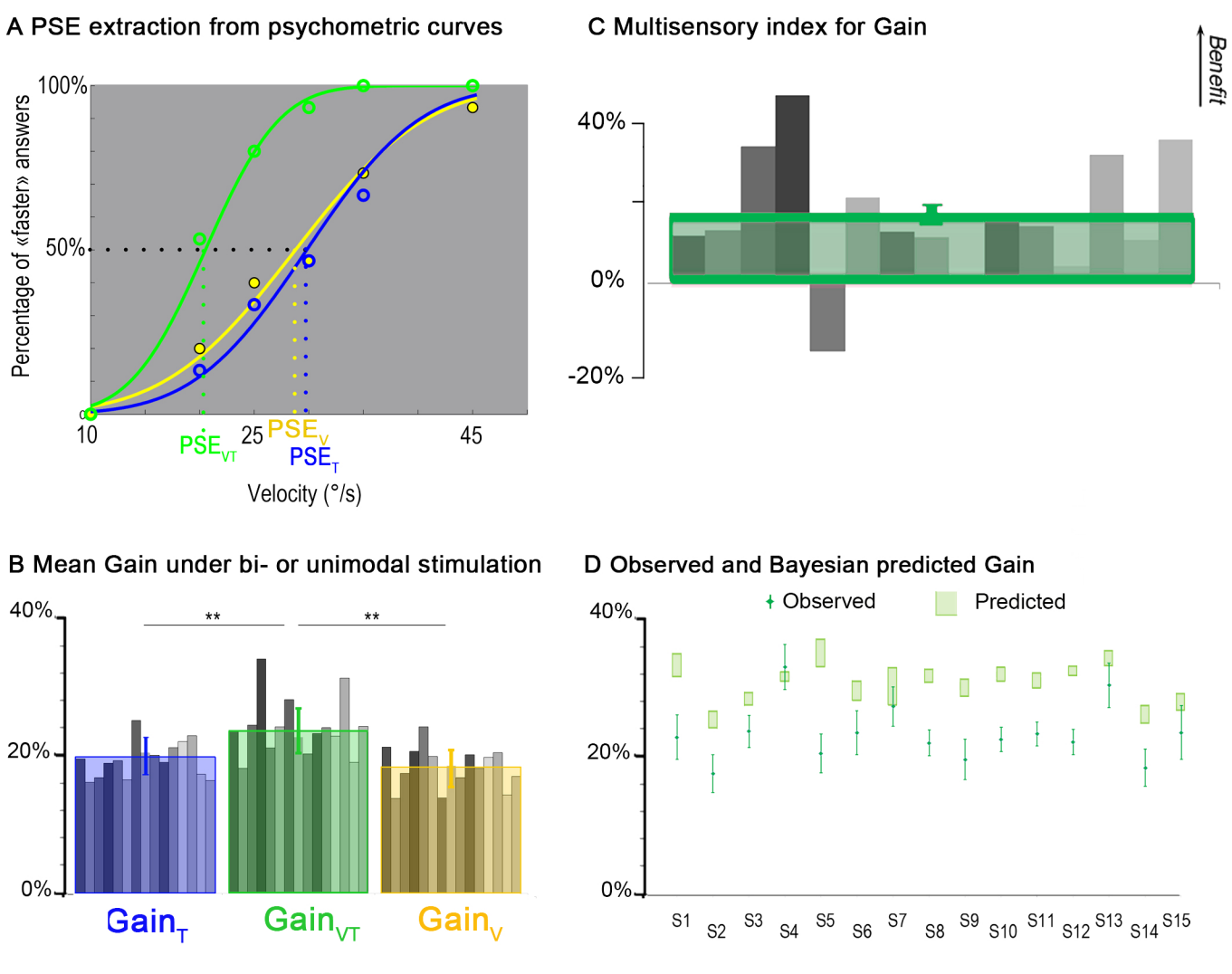
954 **B. Difference between prediction and observation $Gain_{pred}$ - $Gain_{obs}$**: The quantitative difference
955 between model predictions and empirically obtained values of visuo-tactile gain was significantly
956 smaller in the *Noisy* condition compared to the *Standard* condition ($P < .05$).

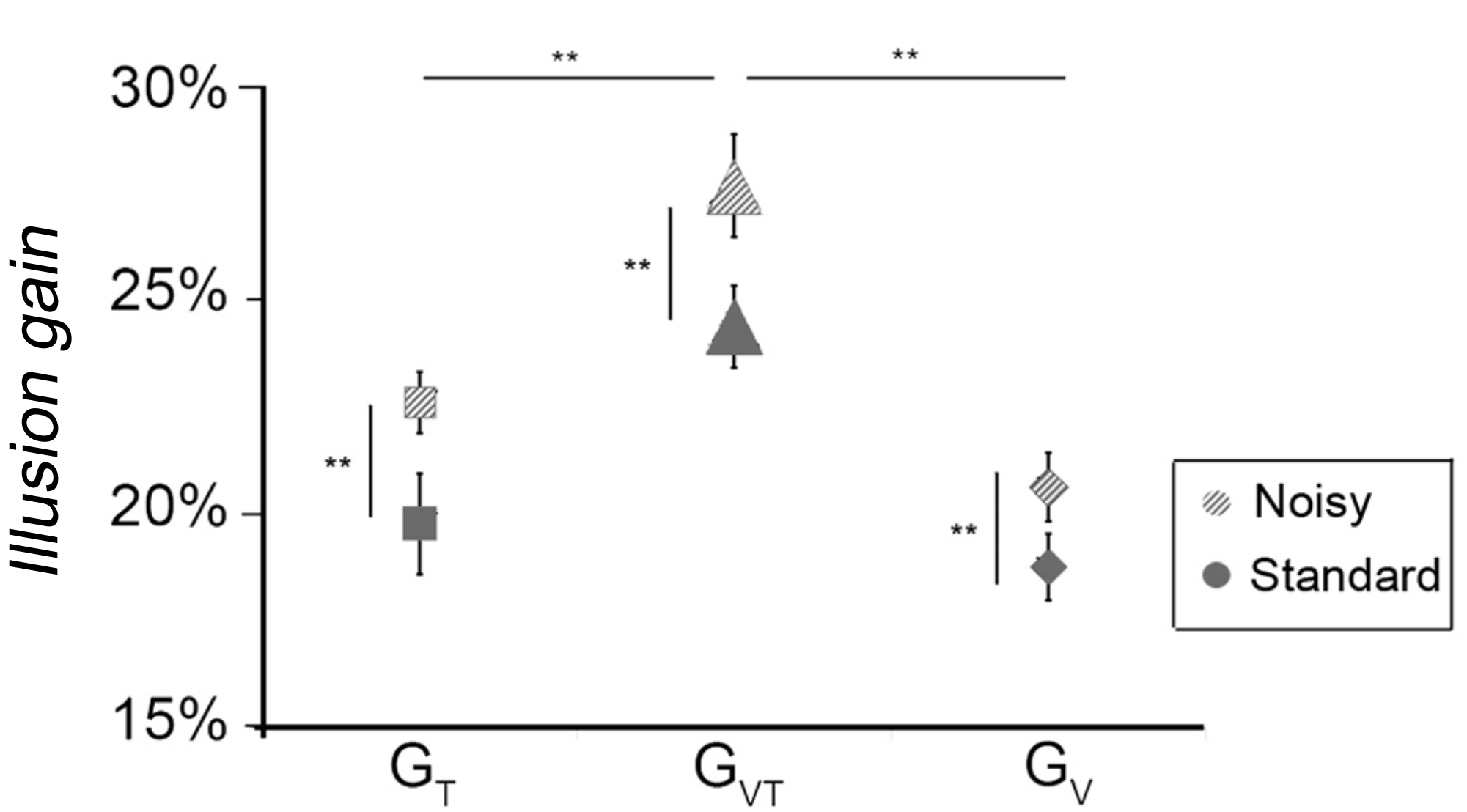

A.
Camera
TOUCH
MP
VISION
Projector
B.
C.
D.

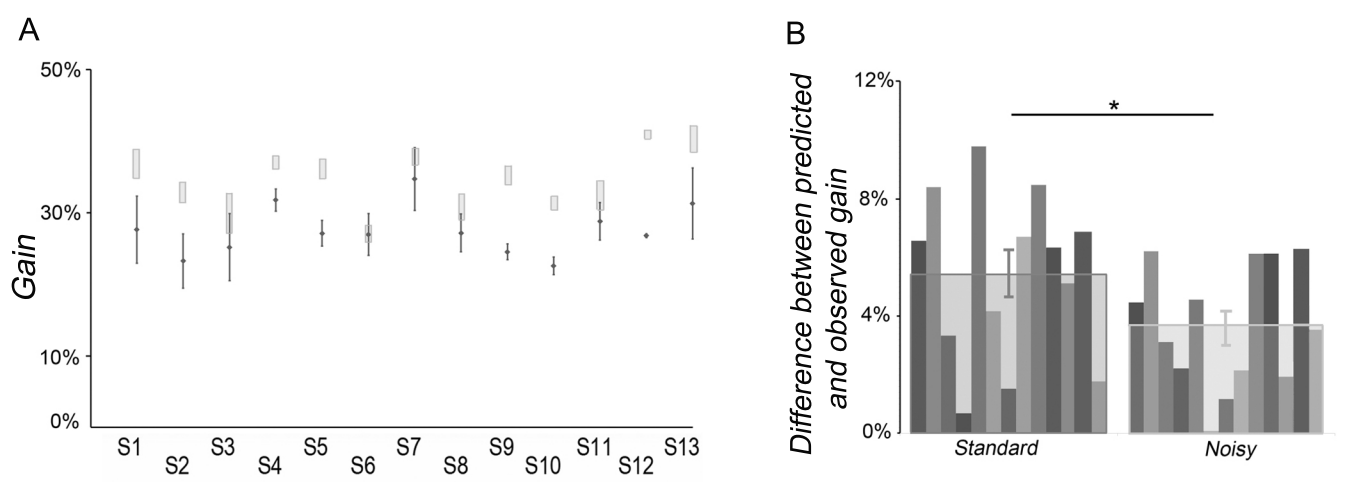

MLE principle
TOUCH
ϑ_T σ_T
VISION
ϑ_V σ_V
ϑ
ϑ
X
BIMODAL
ϑ_{VT} σ_{VT}
$\tilde{\vartheta}$
σ_{VT}
σ_T
σ_V
Stimulation velocity (°/s)


A
Proportion of answers
«test faster than reference»
0.84
0.5
0
Velocity
$\mu_{\psi 1} = PSE$
0.5
$\mu_{Post1} = V_{ref}$
B
Proportion of answers
«test faster than reference»
0.84
0.5
0
Velocity
$\mu_{\psi 2} = PSE + \sigma_{\psi}$
0.84
$\mu_{Post2} = V_{ref} + \sigma_{Post}$


A σ extraction from psychometric curves
Percentage of «faster» answers
84%
50%
σVT
σT
σV
10
25
45
Velocity (°/s)
C Multisensory index for σ
40%
0%
-40%
Benefit
B Mean σ under bi- or unimodal stimulation
°/s 16
12
8
4
0
**
**
σT
σVT
σV
D Observed and MLE-predicted σ
°/s 16
12
8
4
0
Observed
Predicted
S1
S2
S3
S4
S5
S6
S7
S8
S9
S10
S11
S12
S13
S14
S15


A PSE extraction from psychometric curves
100%
50%
0%
Percentage of «faster» answers
10
25
45
PSE_VT
PSE_V
PSE_T
Velocity (°/s)
C Multisensory index for Gain
Benefit
40%
0%
-20%
B Mean Gain under bi- or unimodal stimulation
40%
20%
0%
**
**
Gain_T
Gain_VT
Gain_V
D Observed and Bayesian predicted Gain
Observed
Predicted
40%
20%
0%
S1
S2
S3
S4
S5
S6
S7
S8
S9
S10
S11
S12
S13
S14
S15


Illusion gain
30%
25%
20%
15%
**
**
**
**
**
G_T
G_{VT}
G_V
Noisy
Standard


A
50%
30%
10%
0%
Gain
S1
S2
S3
S4
S5
S6
S7
S8
S9
S10
S11
S12
S13
B
12%
8%
4%
0%
Difference between predicted and observed gain
*
Standard
Noisy